DIFFERENTIATION IN HYDROID COLONIES. II. AGLAOPHENIA.

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In a former paper[1] I called attention to the fact that many species of hydroids change their structural type with age, that is, in the direction of their growth. "Stems straight proximally may become sinuous distally. Branches which alternate during the early stages of colonial development may later originate in pairs. Length and annulation of hydrothecal pedicels, size, proportions and ornamentation of hydrothecæ may similarly vary with the distance from the base of stem or branch." An attempt to analyze the problems in differentiation suggested by these facts was begun, upon a species of campanularian peculiarly well adapted for experimentation. The results reached favored the view that the progressive changes in the differentiation of the individuals of a colony are not dependent upon changes of external conditions, but upon changes of internal conditions; and that these changes are of a physiological character, and do not lead to a conception of *morphological determinants* or *residual germ plasm.*

The bearing of the facts upon the problem of senescence was also suggested. For, on the stem of such a hydroid as *Campanularia* — with a cymose type of budding — the individuals appear as successive generations, forming, at the same time, parts of the whole colony. Accordingly, a comparison of any two individuals might be expected to show a difference in their structure corresponding in some degree to a period of physiological change in the colony equal to their difference in age.

Since the publication of these results, several important papers have appeared expressing radically different views on the relation of natural death and development. Minot (*Pop. Sc. Mo.*, Nov., 1907, p. 472) holds that as cells differentiate they lose something of their capacity to live. Loeb (*Pfluger's Arch.*, 124, 1908, p. 411), after stating this conclusion in chemical terms as follows:

[1] Univ. Cal. Publ., Zoölogy, 2, p. 323.

that the chemical causes of death are identical with the chemical processes that lie at the basis of development itself, differs with it radically. He asserts, as a result of experiments with the eggs of sea urchins, that natural death and development are determined by chemical processes that have absolutely nothing to do with each other.

My own investigations, impeded, among other causes, by scarcity of material, have not yet reached a definite conclusion in this direction, although the results so far obtained are not inconsistent with the results of Loeb's brilliant experiments. Meanwhile, the facts as they appear in seven species of *Aglaophenia*, may be of some service to experimenters interested in the general problem.

As is very well known, a typical colony of the plumularian hydroid *Aglaophenia* closely resembles a feather, of which the shaft is represented by the stem and the vanes by two ranks of alternating branchlets, or hydrocladia, corresponding to barbs. Each hydrocladium is divided by more or less definite nodes into internodes and bears on one aspect — the same in all hydrocladia — a compact series of hydranths, one to each internode, with tooth-rimmed hydrothecæ. Associated with each hydrotheca are three tubular nematophores, a pair laterally placed, to the rear, and one in front in the median line (mesial).

Inspecting such a colony for signs of the differentiation connected so clearly with age in *C. bakeri*[1] one would naturally look for differences associated, first, with the growth of the colony as a whole, second, with the growth of individual hydrocladia. The former might be determined by a comparison of corresponding internodes of different hydrocladia, the latter by a comparison of successive internodes of the same hydrocladium.

In both cases, this procedure has established a correlation between differentiation and growth.[2] Since the picture of the correlation is not equally clear and elaborate in all species studied, I will describe it first for one of the most satisfactory in these respects, namely, *A. octocarpa*.

[1] *Loc. cit.*

[2] See Pearl, Publ. Carnegie Inst. 58, 1907, and, more recently, Ritter, Univ. Cal. Publ. Zoöl., 6, 1909, p. 64.

It should be understood, in examining all the tables and figures which follow in this paper, that they make no pretense to be

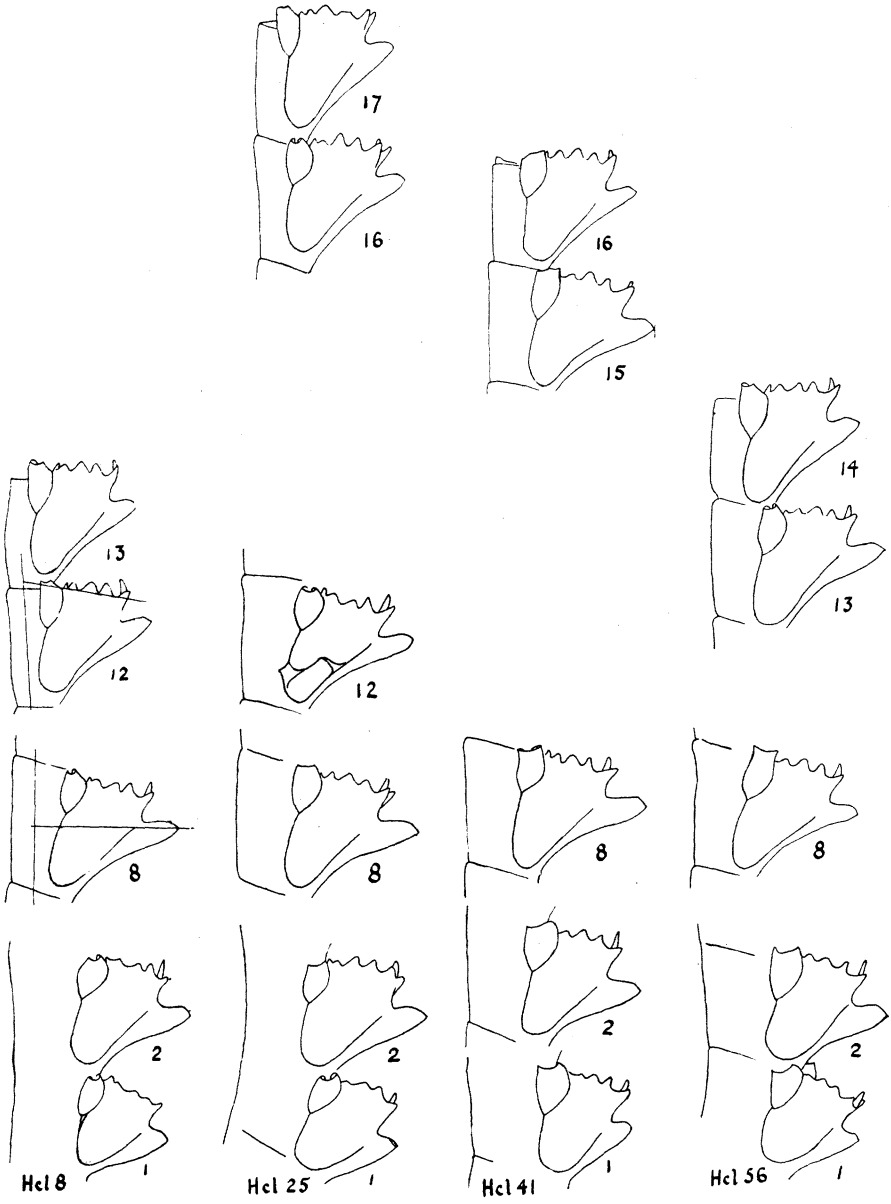

FIG. 1. *A. octocarpa*, × 45.

statistically thorough. They are rather illustrative of certain facts of differentiation that do exist and are capable of experimental analysis.

A. octocarpa. — A glance at the accompanying camera drawings (Fig. 1) will acquaint one with the main differentiating characters on which the present study is based. The four series of figures represent hydrothecæ from four hydrocladia. That they might be representative of the colony, the latter were selected at various levels on the right of the stem, being nos. 8, 25, 41 and 56, in a series of 64,[1] and care was taken that they should be the longest obtainable and, if possible, not damaged at their distal ends. Similarly, the hydrothecæ, drawn in profile, were chosen as representative of the whole hydrocladium, being nos. 1, 2, 8, usually 12, and the terminal two.

In the condensed picture of the conditions throughout the colony thus obtained, certain facts stand out prominently:

1. Each hydrocladium tapers from base to tip.[2]

2. On each hydrocladium, hydrotheca no. 1 is noticeably smaller than the others, and the mesial nematophore associated with it is especially short.

3. From base to tip, the openings of the hydrothecæ become less oblique to the axis of the hydrocladium. This obliqueness may be shown numerically by measuring the angle made with the axis of the internode by a line drawn tangent to the depressions between the first and second, and the third and fourth, lateral marginal teeth on each hydrotheca (12, *Hcl. 8*, Fig. 1). Two series of measurements from different colonies are shown in Tables I. and II.

4. The mesial nematophore reaches its greatest prominence toward the middle of the latter and then declines to the tip. This fact is numerically expressed in Table III., which shows the profile width of each hydrotheca to the point of the mesial nematophore on a line perpendicular to the axis of the internode (see Fig. 1, *hydrocl. 8*, *hth. 8*).

[1] The tip of the colony was wanting.

[2] This, as shown by repeated observations, is independent of the thickening of the perisarc with age. For convenience, neither such thickenings of the walls nor the septal and intrathecal ridges characteristic of the species have been drawn, except in 12, *Hcl. 25*, where the intrathecal ridge is shown.

TABLE I.

Measurements in Degrees of Angle.

Hydrocladium.	Hydrotheca.								
	1	2	8	12	13	14	15	16	17
8	114	110.3	108.2	103	96				
25	103.8	99.3	108	102.8				100	96
41	115.2	109	105				108	99	
56	116.2	116.5	105.5		99	91.2			

TABLE II.

Hydrocladium.	Hydrotheca.				
	1	2	7	11	
1	122	111.5	101.5	89.7	(12 hydrothecæ present)
40	99.7	111.8	101.5	100	(14 " ")
85	111.3	111.2	103.7	100.5	(13 " ")

TABLE III.

Measurements in mm. × 95.

Hydrocladium.	Hydrotheca.								
	1	2	8	12	13	14	15	16	17
8	24	30.5	32	27	25.5				
25	25	32	34	31				29.5	27.5
41	23.5	30	33.5				31.5	29	
56	25.5	30.5	30.5		30.5	27			

The facts formulated above concern the differentiation of internodes of single hydrocladia from various regions of the colony. On further examination, Tables I. and III. suggest that the character under consideration tends to decline from its maximum less rapidly on hydrocladia in the middle region of the colony than on hydrocladia either proximal or distal to them. This suggestion that the colony may have a typical form, exhibiting a differentiation from base to tip, analogous to what is so familiar in the leaves of plants, is supported by series of measurements at the tips of several colonies. One such series is presented in Table IV., in which are given both the length of each theca, through the unpaired or mesial tooth (upper figures), and the width of the theca through the tip of the mesial nematophore (lower figures in italics), as in Table III.

TABLE IV.

Measurements in mm. × 95.

Hydrocladium.	Hydrotheca.																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
3 (from tip)	—	36.5	38	38													
	27	*32*	*32*	*31*													
4 " "	—	37	37.5	37	37												
	—	*33*	*34.5*	*33*	*31*												
7 " "	—	37	—	38.5	38.5	38	38	—	38	36							
	—	*33*	—	*36*	*35*	*35*	*34*	—	*33*	*31*							
10 " "	—	—	37	—	38	—	38	—	—	38.5	—	38	38				
	—	—	*34*	—	*35*	—	*35*	—	—	*35*	—	*31.5*	*28*				
13 " "	32	35.5	38	38	38.5	—	37	—	38	38	38	38	37.5	38.5	37	38	—
	25±	*34*	*35*	*35*	*34*	—	*35*	—	*35*	*35*	*34.5*	*34.5*	*34.5*	*34*	*33*	*30.5*	—

It will be seen that, as the tip of the colony is approached, not only do the hydrocladia possess fewer and fewer hydrothecæ, but the dimension of the latter through the mesial nematophore reaches its minimum more and more rapidly. Since the hydrothecæ, once formed, do not enlarge with age, it is clear that for such colonies as this, there is a limit of growth and a specific form.[1]

A. pluma. — This species not only supports the statements made for *A. octocarpa*, though somewhat less conspicuously, but presents another character (of no value in *A. octocarpa*) by which differentiation in the hydrocladia may be determined, namely, the length of the hydrotheca through the mesial tooth. Fig. 2 presents graphically, in concentrated form, the characters of a single colony so far as they concern the discussion. The measurements taken from the drawings are represented in the accompanying tables. It should be said, in this connection, that these measurements are subject to a certain amount of correction, owing to the great difficulty experienced at times in obtaining true profiles of the hydrothecæ. In hydrocladium no. 25, for instance, the hydrothecæ have suffered a degree of rotation which could not be rectified by the means at my disposal. The application of pressure sometimes suffices, but is very liable to produce more serious distortions. Fortunately, the errors which

[1] According to Table IV., the length of the hydrothecæ does not appear to be a significant dimension in *A. octocarpa*.

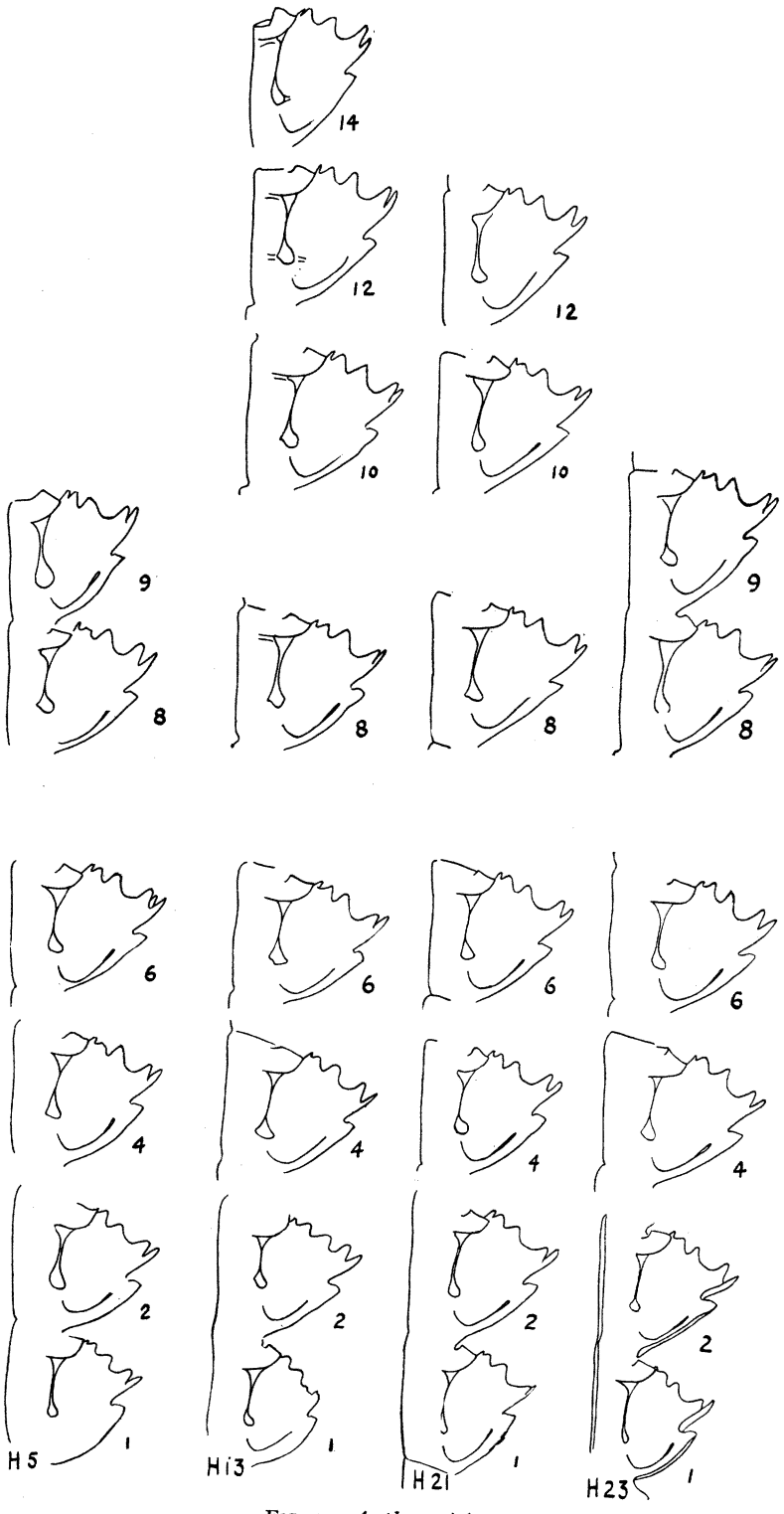

FIG. 2. *A. pluma*, × 45.

thus appear to be unavoidable, do not disturb in any essential respect the conclusions based on the measurements.

Differentiation within the several hydrocladia will first be considered.

In Table V., appear the measurements of the length of the mesial nematophore along a line perpendicular to the axis of the internode (upper figures) and the width of the hydrotheca to the tip of the nematophore along the same line (lower figures). The width of the hydrotheca along the line chosen varies, as shown by the table, independently of the length of the nematophore along the same line. Neither character is of much value

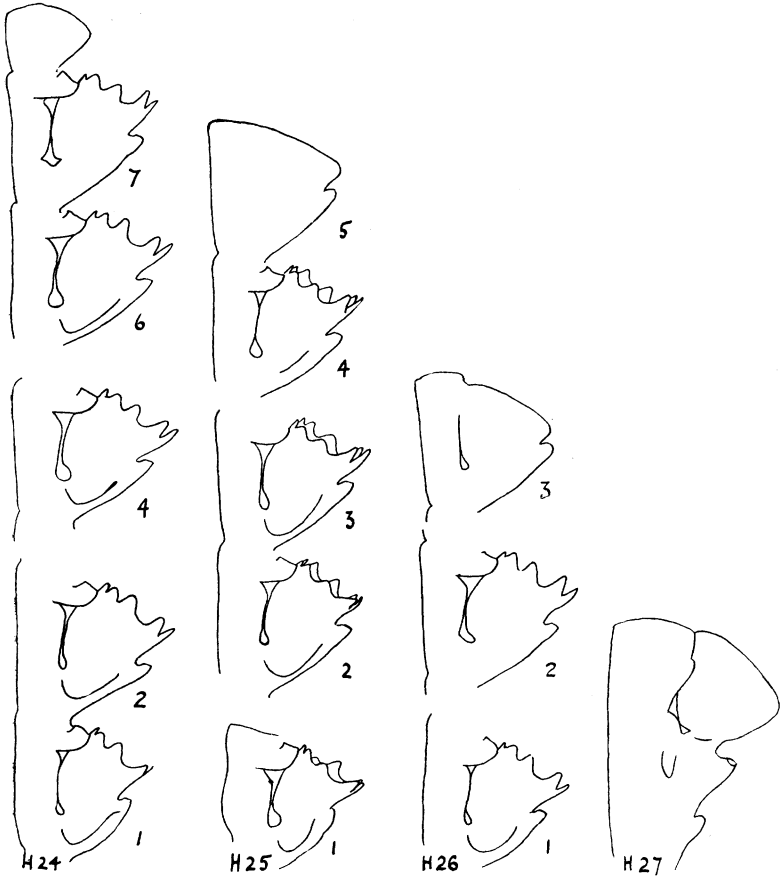

FIG. 2

to the experimenter in this species, owing largely to the slight degree to which the nematophore projects, and the narrow range of its variation in length, in fractions of a millimeter, as compared with the fluctuations in width of the hydrothecæ. There is no doubt, however, that the nematophore tends to vary, as in *A. octocarpa*, with the growth of the hydrocladium, its maximum length lying in the middle region of the latter.

TABLE V.

Measurements in mm. × 95.

Hydrocladium.	Hydrotheca.													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
27	bud													
26	3.3 21.3	3.5 25	bud											
25	—	*4.5* 23.5	4 24.5	4 23	bud									
24	3.4 19.3	4.2 23.5		*4.6* 24.5		4 25.5	3.8 24.5	bud						
23	3.8 19.5	3.8 22		*4.5* 25.5		*4.4* 26.5		3.5 24.5	3.8 24.5	bud				
21	3.8 19.7	3.2 23		3.5 23		*4* 23.2		3.5 24.5		3 24.5		3.8 24.5	bud	
13	2.7 18.5	3 21.5		3 23.5		3.5 24		*3.9* 24		3.6 23.5		3.2 24.5		2.8 21.5
5	3.3 19.5	4 22.5		3.5 24		*4.3* 25		4 25	3 21.5					

The obliqueness of the openings of the hydrothecæ is recorded in Table VI., in degrees of angular distance, as for *A. octocarpa*, with this exception, that the line defining the obliqueness is drawn tangent to the depressions between the mesial and first lateral, and the third and fourth laterals (the margin having but nine teeth). This is a more stable standard, but could not be utilized in *A. octocarpa*, owing to the shape of the hydrotheca in that species.

With slight irregularities, the chief among them being connected with the variability of hydrotheca no. 1, the obliqueness diminishes toward the distal end of each hydrocladium.

TABLE VI.

Measurements in Degrees of Angle.

Hydrocladium.	Hydrotheca.													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
27	bud													
26	128	125.5	bud											
25	128	131.5	125.5	126	bud									
24	129.8	130		128.5		123.3	*119.3*	bud						
23	127.5	129.8		129.3		125.5		123.5	*119.3*	bud				
21	130.3	129		120		120		120		119		*115.3*	bud	
13	—	125		128.2		123		124		121.5		117		*115*
5	133	131		121.5		121.5		120.2	*115*					

The lengths of the hydrothecæ, taken through the mesial tooth, are recorded in Table VII. There is a definite tendency to increase in length toward the distal end of each hydrocladium, the longest hydrotheca, however, being subterminal.

TABLE VII.

Measurements in mm. × 95.

Hydrocladium.	Hydrotheca.													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
27	bud													
26	30.5	?	bud											
25	27.5	31.5	*34.5*	?	bud									
24	30.5	33.5		34.2		*36.5*	bud							
23	28	30.5		34.5		36		35	*36.5*	bud				
21	31	33		32		33		35+		*36*		35	bud	
13	—	30		31.5		34.5		34		36		*37.3*		32.5
5	—	29.5		33		34.5		*35.5*	33.5					

In Table VIII., the widths of the hydrothecæ previously used have been taken along the line defining the obliqueness of the opening of the hydrothecæ. As the figures show, this character is too variable to be very useful to the experimeter. Nevertheless, in common with the characters considered in the three tables

TABLE VIII.

Measurements in mm. × 95.

Hydrocladium.	Hydrotheca.													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
27	bud													
26	20	*22*	bud											
25	18	18.7	*20.5*	20	bud									
24	17.5	21		*21.5*		21	20	bud						
23	19	21.2		21		*22*		21.5	21	bud				
21	17	20.5		20		21.5		*22.3*		21		22	bud	
13	—	20.5		20.5		20.5		20.5		21.2		*22.3*		20.5
5	17.5	20		20.2		*22*		*22*		19.7				

just preceding, it aids in establishing the fact that colonies of *A. pluma*, like colonies of *A. octocarpa*, have a limited growth and a specific form, the hydrocladia, with respect to given characters, differing in different regions. To appreciate this fact, it is only necessary to note the position (1) of the maxima on the various hydrocladia in Tables V. (upper figures), VII. and VIII., and (2) of the minima in Table VI., especially in connection with hydrocladia 5, 13, 21, 23 and 24.

A. inconspicua.[1]—This small species is represented most scantily in the collections of the University of California. No conclusions can be offered concerning the form of the colony as a whole, as observations on the tip of a mature colony are at present out of the question. From the drawings (Fig. 3) of the internodes from two hydrocladia, however, and the measurements based upon them, Tables IX. and X., the species possesses admirable characters for experimental work, in the prominence of the mesial nematophore and the obliqueness of the hydrothecal opening.

These figures are typical, similar measurements from other hydrocladia and other colonies giving results that vary, within the hydrocladium, in no essential respect from them. It may be said that the hydrotheca at the base of each hydrocladium is especially variable and often differs conspicuously from those distal to it in size, shape, marginal dentation, and position on the

[1] Torrey, Univ. Cal. Publ., Zoöl., 1, 1902; *ibid.*, 2, 1904.

hydrocladium (owing to a slight rotation out of the plane of the other hydrothecæ). Nothing sufficiently definite can be said about the length or thickness of the hydrothecæ. There is a perceptible increase in size of the hydrothecæ in *Hcl. 21*, toward the tip. It is much less in the other hydrocladium; and meas-

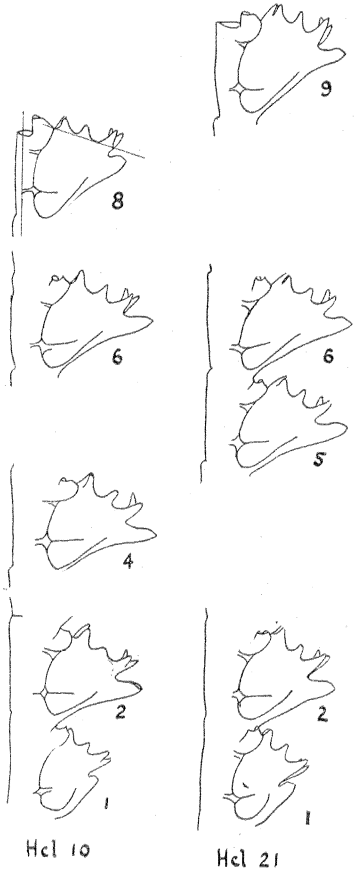

FIG. 3. *A. inconspicua*, × 45.

urements of others show that it is not characteristic and typical, for either dimension.

A. lophocarpa. — The few colonies of this species at hand are all imperfect, both as to stems and hydrocladia. However, the hydrocladia taper from base to tip, the first hydrotheca on each

TABLE IX.

COLONY WITH 28 HYDROCLADIA.

Measurements, in mm. × 95, of the profile width of each hydrotheca in Fig. 3 to the point of (1) the mesial nematophore on a line perpendicular to the axis of the internode (lower figures), and (2) the length of the mesial nematophore on the same line (upper figures).

Hydrocladium.	Hydrotheca.						
	1	2	4	5	6	8	9
10	2.5 16	7.3 26	8.2 29.5		8 24	4.8 24	
21	4.5 17	7 26		8.8 28.5	7.6 29		7.5 27.5

TABLE X.

Same colony, showing angles made with the axes of their internodes by the planes of the hydrothecal openings, the latter being represented in each case by a line tangent to the depressions between lateral marginal teeth 1 and 2, and 4 and 5 (see *Hcl. 10, hth. 8*).

Hydrocladium.	Hydrotheca.						
	1	2	4	5	6	8	9
10	125.5	121.3	122		114	105	
21	132.3	130		123.2	121		105.3

is smaller than the others, and there is a distinct tendency toward a reduction of the obliqueness of the hydrothecal opening, from base to tip. The mesial nematophore, also, projects farther from the hydrotheca in the intermediate internodes than at either extreme of the hydrocladia.

A. struthionides. — The obliqueness of the hydrothecal openings in each hydrocladium is practically constant in this species (Fig. 4). As in *A. octocarpa*, however, each hydrocladium tapers from base to tip, and the mesial nematophore is most prominent between the extremes. The prominence of the nematophore is, perhaps, of all the characters, most useful to the experimenter. The measurements in Table XI. show that the length of the nematophore along a line passing through its tip and perpendicular to the axis of the internode, varies independently of the width

of the hydrotheca along the same line from the base of the nematophore (see Fig. 4, *BHcl, hth.12*).

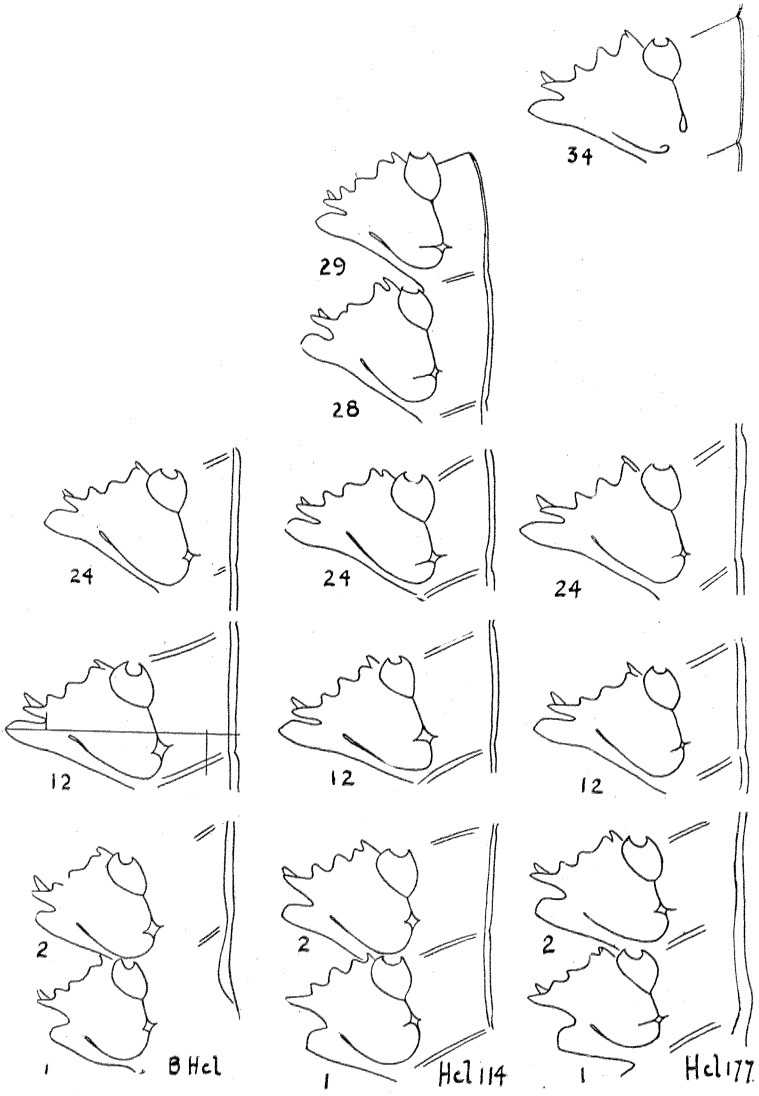

FIG. 4. *A. struthionides*, × 45.

Neither this nor the following species lends itself easily to a determination of colonial differentiation, as does *A. pluma*. Both are variable, often luxuriant growers. Colonies of *A.*

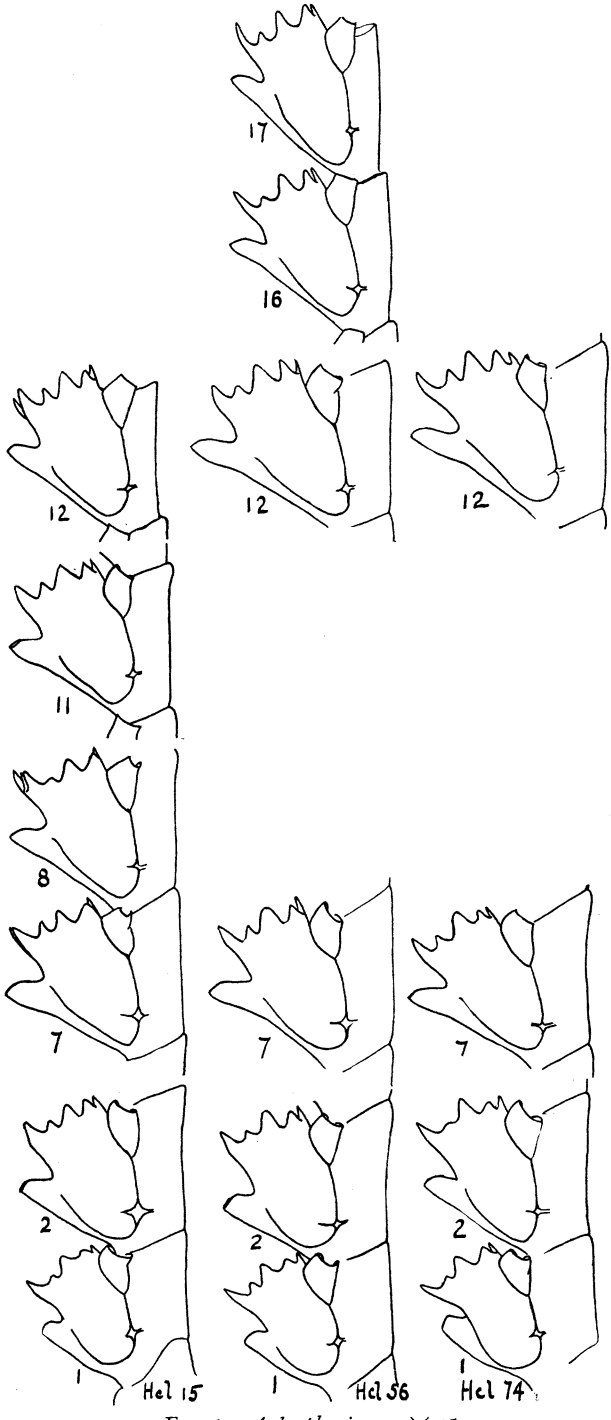

FIG. 5. *Aglaophenia* sp., × 45.

TABLE XI.

Measurements in mm. × 95.

		Hydrotheca.			
		2	12	24	34
Hcl. at base	1. Base of nem. to tip	5	11	9	
	2. Base of nem. to rear of theca	26.4	29.5	28.5	
	3. Value of fraction 1 ÷ 2	.19	.37	.31	
" 114	1.	8.2	11.3	9.9	
	2.	27	28.7	28.6	
	3.	.30	.39	.35	
" 177	1.	8.2	11.3	12	9.5
	2.	24	27.8	30.7	32.3
	3.	.34	.40	.39	.29

struthionides may exceed 23 cm. in length. *Aglaophenia* sp. has a particularly stringy, sprawling habit. The character is of no practical value in the present connection.

Aglaophenia sp. — This species differs from *A. struthionides* in no particulars essential to the present discussion.

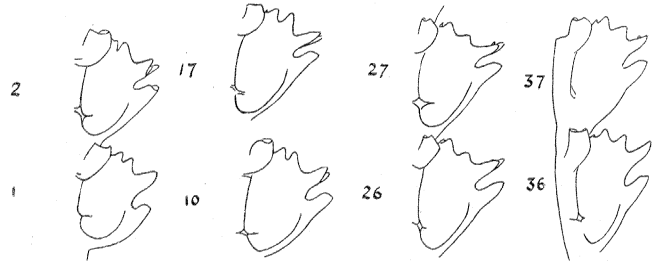

FIG. 6. *A. diegensis*, × 45.

TABLE XII.

Distance from tip of nematophore to rear of theca along perpendicular to axis of internode. Measurements in mm. × 95.

Hydrocladium.	Hydrotheca.							
	1	2	7	8	11	12	16	17
15	24	31	34.5	33	32	31		
56	24.5	30	35.5			40	32	30
74	25	29.5	34.5			37.5		

Hydrocladium 74 is incomplete, hydrotheca 12 not being terminal.

A. diegensis. — Of all the species, this is the most irregular. It agrees in general, however, with *A. octocarpa.* The hydrocladia taper distalward; the first hydrotheca is small and more or less irregular, with short mesial nematophore; the mesial nematophore is most prominent between the extremes of the hydrocladia; and there is a slight lessening of the obliqueness of the hydrothecal openings distalward. Fig. 6 is from a single hydrocladium.

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